Changes in the Zooplankton of Onondaga Lake: Causes and Implications[1]

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ABSTRACT

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The zooplankton assemblage of ionically polluted, culturally eutrophic Onondaga Lake was monitored over the 1979-1989 interval, and compared to surveys conducted in 1968 and 1978. A major shift in the assemblage was apparent by 1987, soon after the closure (1986) of an industrial discharger of ionic (Cl^-, Na^+ and Ca^{2+}) waste. Species richness increased from 8 to 18 common species, and more efficient grazers, large-bodied cladocera and the calanoid copepod *Diaptomus siciloides*, became dominants. Until 1987, a single cyclopoid copepod, *Cyclops vernalis*, was the dominant component of zooplankton biomass. The most likely cause for the shift in the zooplankton assemblage of the lake is the reduction in salinity, and attendant precipitation of calcium carbonate, associated with the closure of the industry. Improved clarity in the lake, manifested largely as intervals of dramatic increases described as "clearing events", observed annually since 1987, has been attributed to the shift to more efficient grazers. The increased grazing pressure, particularly from large daphnids, may also be responsible for the return of late summer nuisance blooms of filamentous cyanobacteria, not observed in the lake since the early 1970s.

Key Words: zooplankton, ionic waste, diversity, species richness, daphnid, clarity, Secchi disc, grazing, cyanobacteria.

Zooplankton are often the most important food of many fish species and are highly sensitive to ambient conditions, making the zooplankton community both a good indicator of environmental quality and an important consideration for lake and reservoir managers. The composition of the zooplankton community is influenced by various features of water quality, predation by planktivorous fish, and the composition of the phytoplankton community. The structure and activity of the herbivorous zooplankton community can, in turn, exert substantial feedback by influencing the composition and biomass of the phytoplankton community (McCauley and Briand 1979, Porter 1977), and thus may impact on the public's perception of water quality by influencing water clarity and the occurrence of nuisance algae (e.g., filamentous blue-greens or cyanobacteria (Svensson and Stenson 1991)).

Here we document the major changes in the zooplankton community of polluted, culturally eutrophic, Onondaga Lake, over the period 1969-1989. This analysis includes earlier findings (Meyer and Effler 1980, Waterman 1971), but emphasizes previously unreported results of monitoring for the 1979-1989 interval. Likely causes and implications of the dramatic shift in the zooplankton community are identified based on analysis of concurrent monitoring data for other biological communities and water quality parameters.

Study System

Onondaga Lake is a dimictic, alkaline, hardwater (Effler and Driscoll 1985), urban lake of medium size (area of 12 km²), with a high flushing rate (average of 3.9 flushes/y; Effler and Hennigan 1996), that borders Syracuse, NY. The history of the development of this area, the lake's setting, morphometry, hydrology, and selected features of its degraded state, have been reviewed in this issue by Effler and Hennigan (1996). The lake's culturally eutrophic status is largely a result of effluent discharged from an adjoining domestic waste water treatment facility (METRO; Doerr et al. 1996, Effler et al. 1996a, Effler and Doerr 1996); 60% of the present external load of phosphorus (P) is from the METRO discharge (Effler et al. 1996a). Despite a 5-fold reduction in P loading from this facility since 1977, and concomitant reductions in lake concentrations (Effler et al. 1996a), only a small degree of nutrient limitation is presently experienced by the lake's phytoplankton community (Connors et al. 1995; i.e., other factors such as light and temperature are regulating (e.g., Field and Effler 1983)). Nuisance blooms of filamentous cyanbacteria were common in the lake until a local ban on high-P detergents went into effect in 1971 (Sze 1980, Sze and Kingsbury 1972). The resulting increase in the nitrogen/P ratio in the productive layer is believed to have been responsible for the temporary elimination of cyanobacteria from the lake (Auer et al. 1996), but the recurrence of the filamentous blue-green algae in the lake was noted beginning in 1986 (Auer et al. 1996), in the absence of changes in nutrient conditions. *Aphanizomenon flos-aquae* emerged as a dominant form in the late summer phytoplankton assemblage by 1990 (Auer et al. 1996). Nuisance conditions had substantially worsened by 1994, with the filamentous cyanobacteria bloom extending to 4 months (Makarewicz et al. 1995).

A soda ash/chlor-alkali manufacturing facility located on the western shore of Onondaga Lake operated from 1884 to 1986 (February) and had pervasive impacts on the lake (Effler 1987, 1996). As a result of the ionic (Cl^-, Na^+ and Ca^{2+}) pollution associated with soda ash production, the salinity of the lake (Doerr et al. 1994, Effler 1996) and the rate of $CaCO_3$ precipitation (Driscoll et al. 1994, Womble et al. 1996) were artificially high. Most of the inorganic particles in the lake before (Yin and Johnson 1984) and after (Johnson et al. 1991) closure of the facility have been calcium carbonate ($CaCO_3$). The elevated rate of $CaCO_3$ precipitation (and deposition) was linked to the Ca^{2+} component of salinity. Thus, the abrupt reduction in the salinity of the lake (Fig. 1a) that followed closure of the facility (Doerr et al. 1994, Effler et al. 1990) was
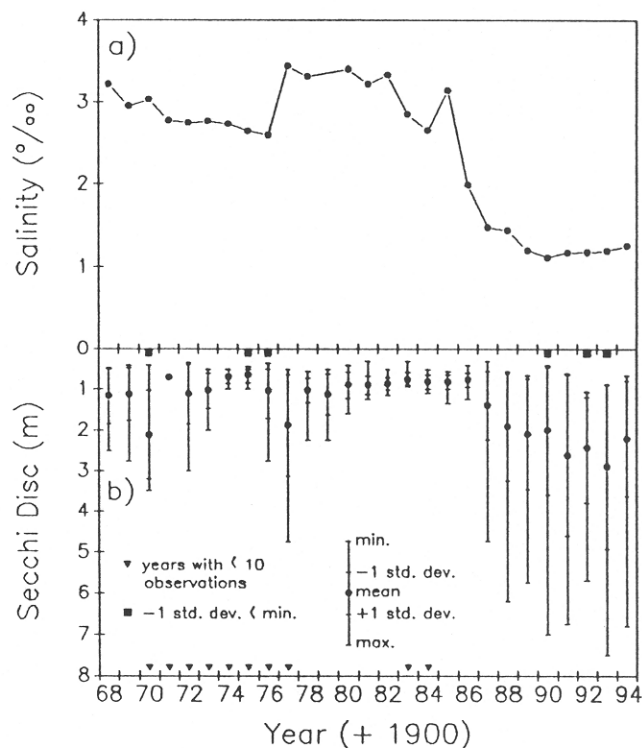

Figure 1.–Time series of yearly conditions in Onondaga Lake: a) salinity, and b) summertime Secchi disc transparency, mean, range, and standard deviation.

accompanied by an abrupt reduction in $CaCO_3$ deposition (Womble et al. 1996). The average salinity before closure of the plant (1968-1985) was about 3‰ (Fig. 1a). Species diversity of various aquatic communities, including zooplankton, is strongly reduced at this salinity (Remane and Schlieper 1971). The USEPA (1974, p.34) indicated "The chloride/salinity levels of the lake (before closure of the soda ash/chlor-alkali facility) approach concentrations at which one would expect to find the smallest species diversity; that is, the chloride/salinity level is near the upper limit for freshwater organisms and near the lower limit for marine species." Limited watercolumn $CaCO_3(s)$ concentration data (Effler 1996) indicate that $CaCO_3(s)$ levels have exceeded those known to inhibit daphnid reproduction (~0.8 mm³/L; Vanderploeg et al. 1987).

Transparency during summer (May-September) over the 1979-1986 interval (and in several earlier years) was extremely low and varied little within years or among years (Fig. 1b). Abrupt dramatic increases in clarity, described as "clearing events" (Auer et al. 1990), attributable to major reductions in the concentration of phytoplankton and other particles (Perkins and Effler 1996), were manifested in most years in the 1970's and annually since 1987 (Fig. 1b). "Clearing

events", or clear water phases, are common in temperate lakes (Lampert et al. 1986). The intensity and duration of the events in Onondaga Lake since 1987 have been greater than observed in earlier years (Fig. 1b), and this distinct shift in clarity coincides with the major reduction in salinity (Fig. 1). We hypothesize that the shift in clarity was triggered largely by the salinity reduction and that it was mediated by the shift in the zooplankton assemblage documented herein.

Methods

The sampling program established in 1978 (Meyer and Effler 1980) was continued annually through 1981, resumed in 1985, and continued through 1989. Sampling was weekly from spring through early fall in most years, except for 1985 and 1987 when sampling was conducted monthly and biweekly, respectively. The earlier program of Waterman (1971) was also based on weekly sampling.

Zooplankton were collected by vertical net hauls at the south basin station utilized for previous zooplankton (Waterman 1971, Meyer and Effler 1980) and on-going water quality monitoring studies (Effler 1996). This site has been found to be generally representative of lake-wide conditions (Effler 1996). Plankton sampling, identification, and quantitative analysis generally followed the protocols established by the USEPA Great Lakes National Program Office for the Great Lakes Surveillance Program (e.g., Makarewicz 1987). A 12 cm diameter 73 um mesh Wisconsin-style plankton net was towed from 10 m to the surface at the study site. Samples were field preserved in a 4% formalin solution. Net efficiency was assumed consistent from year to year in the study and no correction factor was applied for the analysis presented here.

Quantitative analysis of zooplankton samples was conducted at 30X using a Bogarov counting tray. At least 200 individuals of the major forms were counted in each sample. Density estimates were converted to biomass estimates through the use of conversion factors developed from published values and from empirically determined values (Dumont et al. 1975, Makarewicz and Likens 1979, Yan and Strus 1980, Siegfried (unpublished)).

Replicate identifications were made on all samples, i.e., a second analyst examined each sample to confirm species identification. Replicate counts were made on samples selected each month to evaluate the precision of quantitative analysis. Relative percent difference was within precision goals (20%), for all replicate counts of common species. Species were considered common if they accounted for more than 5% of total abundance,

and were considered a dominant member of the plankton assemblage if they accounted for more than 20% of total abundance.

The structure of the Onondaga Lake zooplankton community was examined by principal components analysis. Relative species biomass values (%) for each available date were arcsine transformed and the principal components extracted from the correlation matrix without rotation. Patterns in zooplankton community composition were related to available limnological variables by calculating Pearson correlation coefficients between collection scores on the principal components and limnological variables, i.e., dissolved oxygen, Secchi disc transparency, chlorophyll a, turbidity, the $CaCO_3$ component of turbidity, and depth of thermocline. Statistical analysis was facilitated by use of Crunch Interactive Statistical Package (CRISP 1986).

Results and Discussion

Zooplankton Species Assemblage

The zooplankton assemblage reported from Onondaga Lake has increased from 8 to 18 species over the period of record (Table 1). The increase in rare species (Table 1) is attributable to an increase of the number of collections from the lake. Most of the additions to the species assemblage represent detection of a rare species, but occasionally a species new to the lake is detected and later becomes a dominant member of the community. *Diaphanosoma leuchtenbergianum* is a good example; this cladoceran was not reported by Waterman (1970) or by Meyer and Effler (1980) and did not appear in zooplankton samples until 1986, when it was first detected and subsequently became a numerical and standing crop dominant of the fall community in the same year. It was consistently found to be a dominant member of the community in each of the subsequent years of study.

The cladoceran assemblage of Onondaga Lake has changed dramatically over the period of record. *Ceriodaphnia quadrangula* and *Daphnia similis* were the only cladocerans reported as community biomass or density dominants in Onondaga Lake in 1969 (Waterman 1971). *Ceriodaphnia* continued to be a numerical and biomass dominant of the community throughout the period of record, but *Daphnia* was not even found in the lake during some study intervals. *D. pulex/pulicaria* became an important component of the zooplankton community in 1986 and continued to be a density/biomass dominant through 1989.

Table 1.–Zooplankton assemblage of Onondaga Lake, 1969-1989 (x = present, i.e., occurred in at least one sample but not a dominant in any of the samples, C = common, i.e., occurred as a dominant in at least one sample).

Taxon	1969[1]	1978[2]	1979-81[3]	1986-89[3]
CLADOCERA				
Alona affinis		x		
Bosmina longirostris	x	x	x	C
Ceriodaphnia quadrangula	C	C	C	C
Chydorus sphaericus	x	x		
Daphnia galeata		C	C	x
Daphnia pulex (*pulicaria*)	C	C		C
Daphnia similus	C			
Diaphanosoma leuchtenbergianum				C
Eubosmina coregoni				x
Leptodora kindtii				x
COPEPODA				
Diaptomus sicilis	x	x		
Diaptomus siciloides				C
Cyclops bicuspidatus	C	C		x
Cyclops vernalis	C	C	C	C
Mesocyclops edax	x			x
ROTIFERA				
Ascomorpha sp.			x	
Asplanchna sp.	x	C		
Brachionus angularis			C	
Brachionus calyiflorus		C	C	C
Brachionus plicatus		x		
Brachionus variabilis			C	
Brachionus sp.	C	C		
Filinia longiseta	x	x		C
Filinia terminalis				C
Kellicottia bostoniensis			x	C
Kellicottia longispina			C	C
Keratella c. cochlearis	x		x	x
Keratella c. robusta		x	C	
Keratella c. tecta			x	
Keratella hiemalis	C	C		
Keratella quadrata		C	x	C
Keratella testudo			C	C
Keratella valga	x			
Nothalca squamula				x
Ploesoma truncatum				x
Polyarthra remata			C	C
Polyarthra sp.	C	C		
Synchaeta sp.		C		
Trichocerca multicrinnis				x

1 - Waterman 1971　　　　　2 - Meyer and Effler 1980　　　　　3 - this analysis

Two recent additions to the cladocera of Onondaga Lake, *Eubosimina coregoni* and *Leptodora kindtii*, were found in 1989 samples. Neither species was reported from the lake in earlier studies (Table 1).

The copepod assemblage has also changed during the period of record. *Cyclops vernalis* was the only copepod species present throughout the entire study. Other cyclopoid species occurred more sporadically. The calanoid copepod, *Diaptomus sicilis,* was reported as a rare species in both 1969 and 1978 (Waterman 1970, Meyer and Effler 1980), but was not observed in subsequent years. No calanoid copepods were recorded from Onondaga Lake during the 1979-1981 study interval. In 1986, *Diaptomus siciloides* was first observed in the lake and by 1987 had become one of the zooplankton community dominants.

The rotifer assemblage for Onondaga Lake expanded from six species reported in 1969 to fifteen species in the present study, and to more than thirty species following studies of the littoral zooplankton community (Siegfried 1993). Most of the additions prior to 1986 represent the detection of rare species (Table 1). A number of rotifers first observed in the lake during the 1986-1989 study interval have become density/biomass dominants of the rotifer assemblage. The increase in rotifer species richness may reflect recent improvements in water quality conditions.

Zooplankton Community Composition and Biomass

Major changes in the composition and biomass of zooplankton have occurred over the period of record (e.g., Fig. 2). Multiple biomass peaks were evident in each year of study. Biomass maxima were usually recorded in June or early July. The zooplankton community of Onondaga Lake in 1969 was dominated by rotifers through May (Waterman 1971). Dominance shifted to cyclopoid copepods in early June and then to cladocerans from late June through August (Waterman, 1971). Our estimate of mean June-August zooplankton biomass for 1969 was only ~125 ug/L; the lowest for the period of record. The maximum biomass (368 ug/L) was attained in July, with a secondary biomass peak in late August (265 ug/L). In 1969, extremely low zooplankton abundance was reported for the January-April interval and also in December. These low numbers were attributed to low temperatures and reduced phytoplankton abundance (Waterman 1971).

Zooplankton community composition and biomass levels were dramatically different in 1978 compared to 1969. Although rotifers again dominated (> 90% of biomass) the spring community, cladocera biomass was sharply reduced. The change in abundance of large daphnids was particularly dramatic; decreasing from a mean of ~10/L in 1969 to less than 1/L in 1978 (Meyer and Effler 1980). Meyer and Effler (1980) also reported progressive decreases in mean daphnid size over the 1970-1975 interval. Although small cladocera were present in the plankton of Onondaga Lake from June through October 1978, cyclopoid copepods generally accounted for > 60% of the biomass on most collection dates (Meyer and Effler 1980). The mean summer zooplankton biomass was 625 ug/L (Fig. 2a).

Cyclopoid copepod biomass accounted for > 90% of zooplankton biomass from 1979 through 1981 (Fig. 2a-d). Small cladocera were usually present in July and August, generally representing < 10% of total community biomass. Substantial variation in zooplankton biomass was observed in the 1979-1981 interval (Fig. 2b-d). The mean biomass for the May-August period of 1979 was 1340 ± 256 ug/L (mean ± S.E.), the second highest over the period of record. Mean biomass was much lower in 1980 and 1981, 220 ± 21 ug/L in 1980 and 420 ± 29 ug/L, respectively.

Limited samples available for 1985 indicate a zooplankton community similar to that documented for the 1978-1981 interval; cyclopoid copepods account for > 90% of density and biomass. Zooplankton community composition during 1986 was also dominated by cyclopoid copepods throughout the year. Small cladocerans (*Bosmina, Ceriodaphnia,* and *Diaphanosoma*) were common from mid-July through August, and rotifers were common in July (Fig. 2e). Biomass levels remained low in 1986; the peak was about 650 ug/L and the mean was 280 ± 52 ug/L (Fig. 2e).

Zooplankton community composition was dramatically different in the 1987-1989 period, compared to earlier intervals. Beginning in 1987, and continuing through 1989, cladocera and *Diaptomus siciloides* increasingly dominated biomass (Fig. 2f-h). Cyclopoid copepods were dominant in the spring of 1987 and 1988 but were replaced by the calanoid copepod and cladocera by mid-July in 1987 and by mid-June in 1988 (Fig. 2f and g). Cladocera and calanoid copepods dominated zooplankton biomass throughout much of 1989 (Fig. 2g). There has been a distinct shift to dominance by large cladocera, i.e., *Daphnia* spp., which represented less than 1% of zooplankton biomass in 1986 but 39%, 43% and 57% in 1987, 1988, and 1989, respectively. Zooplankton community biomass remained low through the 1987 monitoring period (mean of 285 ± 48 ug/L). The greatest zooplankton standing crop was observed in 1988; mean of 1612 ± 231 ug/L, and maximum of 3070 ug/L. Mean biomass decreased in 1989 to 430 ± 69 ug/L. Biomass maxima generally occurred in late-May to early-June over the 1986-1989 interval.
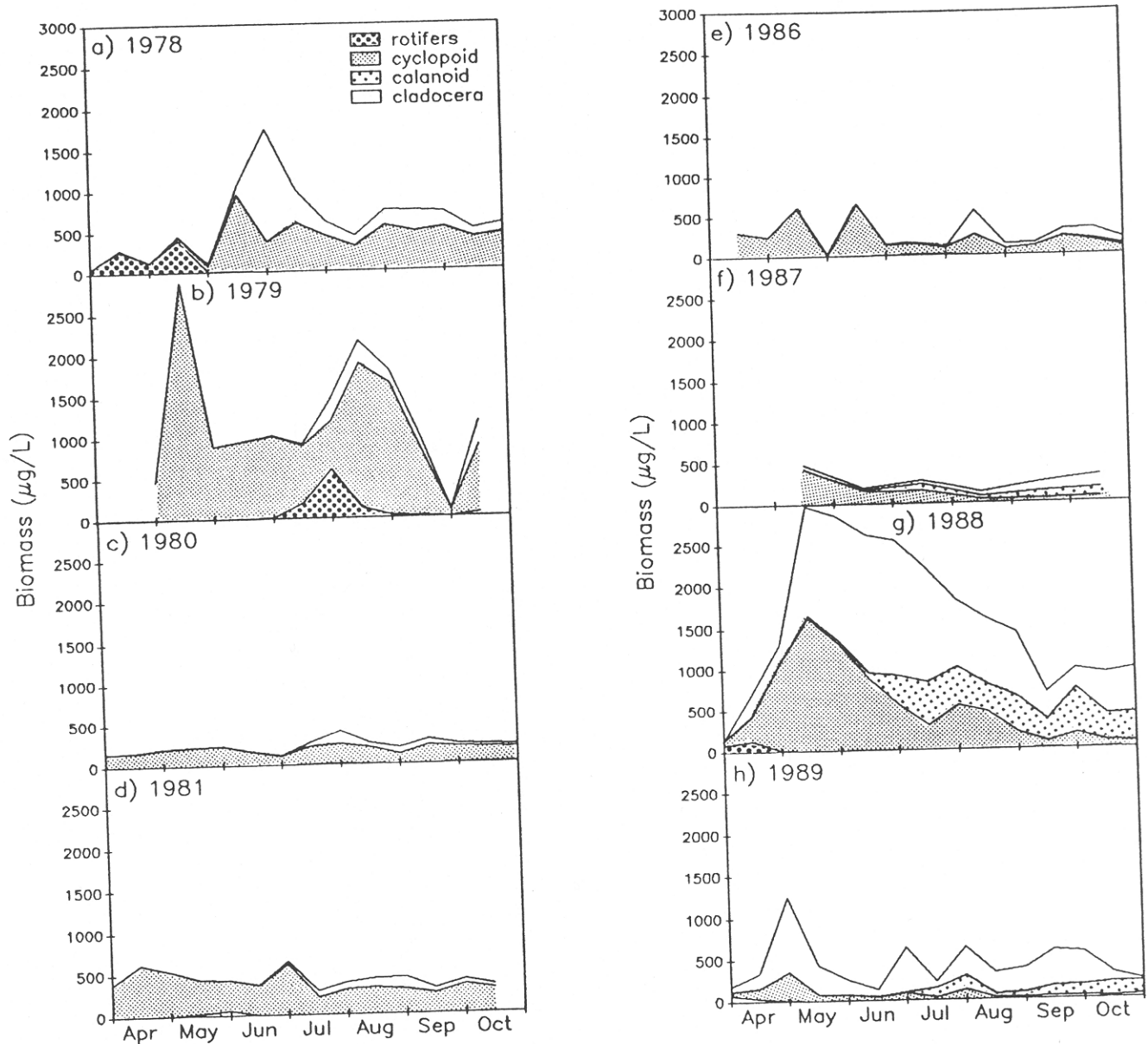
Figure 2.–Temporal distributions of estimated zooplankton biomass in Onondaga Lake, partitioned according to zooplankton group: a) 1978, b) 1979, c) 1980, d) 1981, e) 1986, f) 1987, g) 1988, and h) 1989.

No trend in summer zooplankton biomass was evident over the 1978-1989 period. Mean annual zooplankton biomass fluctuated widely from year to year, from 220 to 1350 ug/L over the 1978-1981 interval and from 285 to 1613 ug/L for 1986-1989 (Fig. 2). The grand mean for the 1978-1981 interval was 596 ± 77 ug/L, while the grand mean for the 1986-1989 study period was 723 ± 108 ug/L.

Time series of concentrations of the most dominant (exclusive of the rotifers) zooplankton (Fig. 3) show that *Cyclops vernalis* has been the most abundant

cyclopoid copepod throughout the period of record, typically accounting for more than 95% of the cyclopoid population. Late spring or early summer maxima have been typical (Fig. 3a) for this largely carnivorous species. Calanoid copepods were virtually absent from 1978 through 1981. *Diaptomus siciloides*, a herbivore, appeared in samples in late July 1986 and was generally abundant in July and August in the 1987-1989 interval (Fig. 3b). *Ceriodaphnia quadrangula* was very abundant in 1978, with peak populations > 1000/L (Fig. 3c). Population maxima of about 200/L were observed in June/July of

other years. Other cladocera were only abundant in the 1986-1989 samples (Fig. 3 d-f). *Daphnia*, the largest herbivorous cladocera of Onondaga Lake, although present in earlier years, was very abundant in 1988 and 1989 (Fig. 3d). Late-summer to fall peaks in *Bosmina* populations (Fig. 3e) are typical in New York lakes
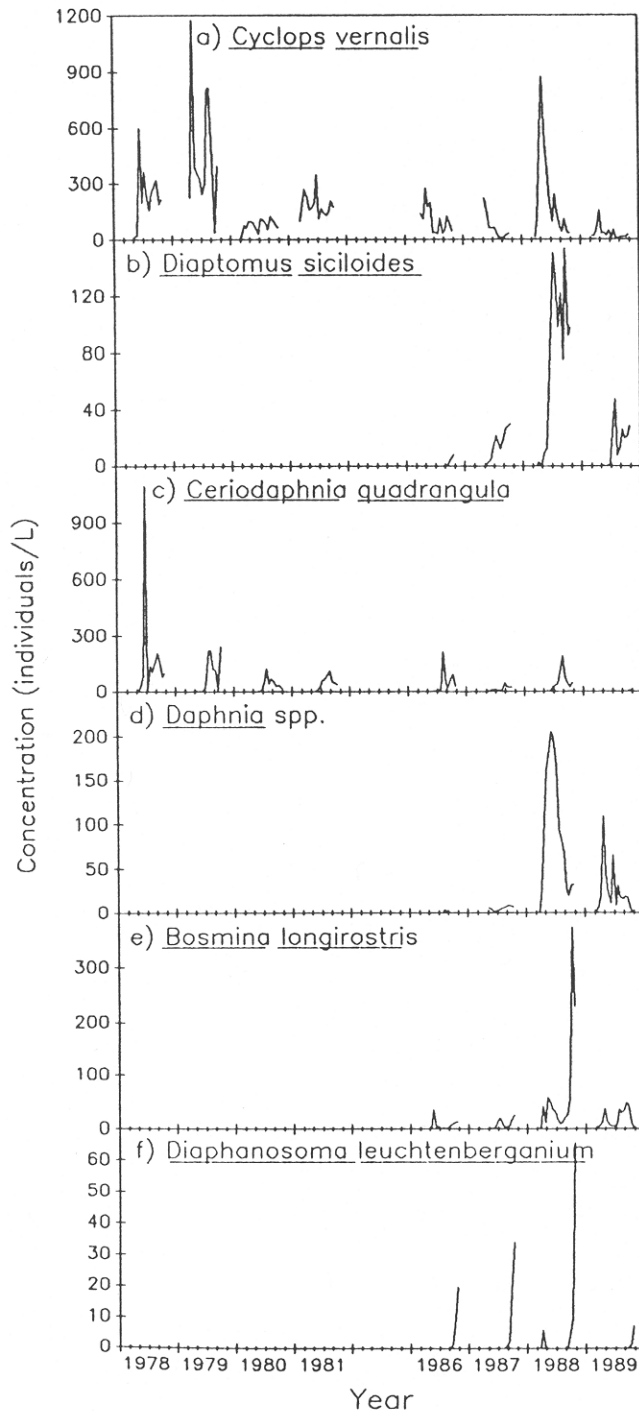
(Siegfried and Quinn 1987, Siegfried unpublished). The occurrence of *D. leuchtenbergianum* in Onondaga Lake was limited to late-summer to fall maxima, except in 1988 (Fig. 3f).

Principal Components Analysis

The four components retained (i.e., eigenvalues > 1.0) in the principal components analysis explained 70% of the variability in zooplankton community composition (Table 2). Twenty-seven percent of the variation in zooplankton community composition is explained by the first extracted component, contrasting samples dominated by *Daphnia* and *Diaptomus* and those dominated by cyclopoid copepods (Fig. 4). The second principal component contrasts samples in which biomass is dominated by small cladocerans
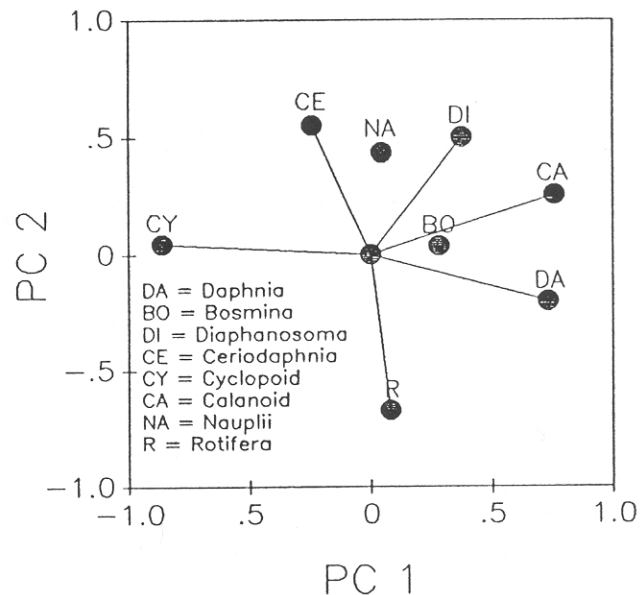
Figure 3.–Distributions of concentrations of selected zooplankton in Onondaga Lake over the 1978-1989 interval: a) *Cyclops vernalis*, b) *Diaptomus siciloides*, c) *Ceriodaphnia quadrangula*, d) *Daphnia* spp., e) *Bosmina longirostris*, and f) *Diaphanosoma leuchtenbergianum.*

Figure 4.–Analysis of structure of Onondaga Lake zooplankton community, first two principal components, relative biomass, summer samples for the 1978-1981 and 1986-1989 intervals.

(*Diaphanosoma*) and those in which rotifers are the dominant component of biomass. The third component retained in the principal components model contrasts samples dominated by *Daphnia* with those dominated by rotifers, while the fourth component contrasts *Bosmina* with *Ceriodaphnia* dominated samples.

Seasonal and annual variations in community composition were examined by plotting mean monthly (May - August) scores for the first two principal components (Fig. 5). The mean monthly scores for 1978-1981, with the exception of May 1978, are closely clustered, with negative scores on principal component 1 and generally positive scores on the second principal component (Fig. 5a). The close clustering of principal

Table 2.–Mean (± standard error) density of commonly occurring crustacean zooplankton of Onondaga Lake, 1978-1981 and 1986-1989.

Species	Density (individuals/L)			
	1978 - 1981		1986 - 1989	
Bosmina longirostris	.0004	(.0003)	25.6	(8.4)
Ceriodaphnia quadrangula	75	(20.7)	24.3	(6.0)
Daphnia spp.	.05	(.02)	102.0	(63)
Diaphanosoma leuchtenbergianum	0		4.0	(2.0)
Diaptomus siciloides	.0002	(.0001)	29.0	(6.0)
Cyclops vernalis	245	(48)	119	(23)

component scores reflects a community dominated primarily by cyclopoid copepods throughout each year of study. The one exception to the clustering of scores, the May 1978 score, reflects the complete dominance of rotifers and thus strongly negative scores on the second principal component (Fig. 5a).

The increasing dominance of *Daphnia* spp., *Diaptomus*, and *D. leuchtenbergianum* from 1986 to 1989 and from May to August of each year is reflected in the plots of principal component scores for this period (Fig. 5b). Scores become increasingly positive on both principal components from May through August of each year. The shift from primarily a cyclopoid dominated community in 1986 to progressively greater dominance by cladocerans and calanoid copepods is reflected in the progressive shift toward more positive scores on the first principal component.

Decreasing turbidity, and accompanying increases in transparency, associated with the shift to a zooplankton community dominated by *Daphnia* and a calanoid copepod are reflected in the correlations of scores on the first principal component with limnological variables. Scores on the first principal component were significantly correlated (r = -0.6) with turbidity and Secchi depth transparency; negatively with turbidity, and positively with transparency (Table 4). Significant negative correlations were also evident with chlorophyll concentrations and calcite turbidity (Table 4). Negative correlations with chlorophyll are associated with the seasonal shift from cyclopoid dominance in the spring, when chlorophyll levels are high, to lower chlorophyll concentrations during periods of cladocera dominance.

The seasonal shift from rotifer dominance in the spring when dissolved oxygen concentrations are high to dominance by small cladocera later in the year when dissolved oxygen is lower is reflected in sample scores on the second principal component. These scores are negatively correlated (P < 0.0001) with dissolved oxygen (Table 4). Scores on the third principal component
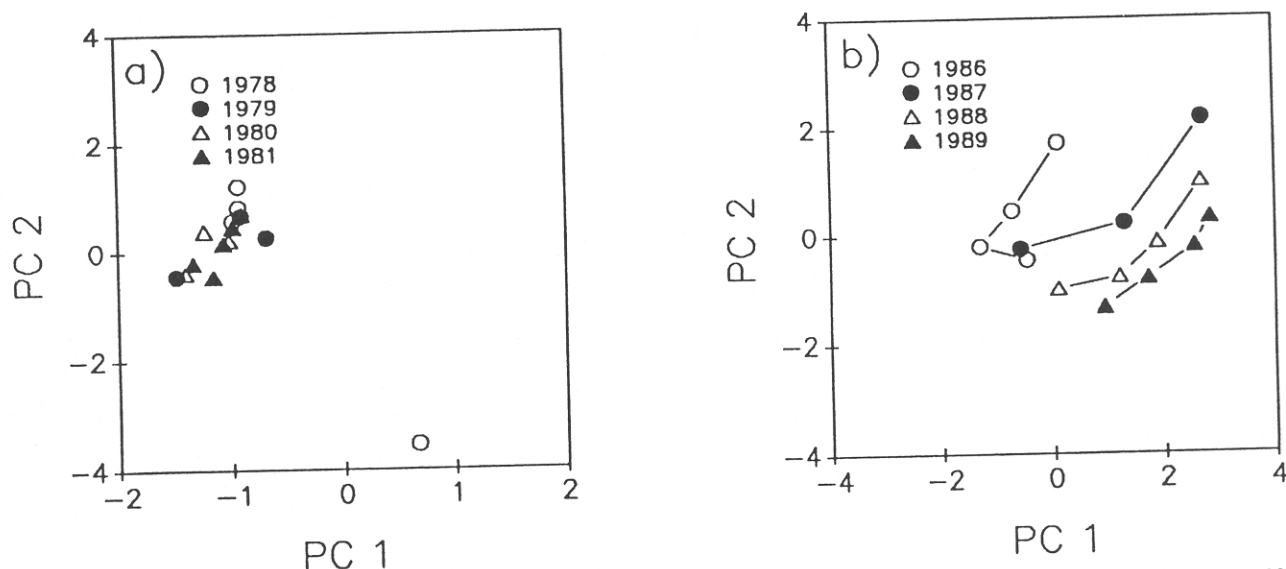

Figure 5.–Plot of mean monthly zooplankton assemblage scores on first two principal components: a) 1978-1981, and b) 1986-1989. Assemblage scores within each year for 1986-1989 interval are connected chronologically, May to August, to illustrate seasonal shifts in scores.

Table 3.–Structure of Onondaga Lake zooplankton community principal components, relative biomass, summer samples 1978-1981 and 1986-1989.

Zooplankton Species	Pearson Correlations with Species			
	PC1	PC2	PC3	PC4
Daphnia	.729	-.203	-.451	-.239
Bosmina	.282	.038	.230	.738
Diaphanosoma	.375	.503	.261	.269
Ceriodaphnia	-.241	.553	.364	-.502
Cyclops vernalis	-.861	.047	-.354	.285
Diaptomus siciliodes	.757	.260	-.132	-.005
nauplii	-.046	.438	.199	-.013
rotifers	.082	-.670	.700	-.089
Eigenvalue	2.133	1.312	1.128	1.015
Percent	26.66	16.40	14.10	12.69
Cumulative	26.66	43.06	57.16	69.85

can be interpreted as reflecting a seasonal shift from rotifers to cladocera, as well as an annual shift toward *Daphnia* dominance as transparency improved between 1978 and 1989 (Fig. 1b).

Reductions in Salinity as the Likely Cause of the Shift in the Zooplankton Assemblage

An important feature of the argument for the reduction in salinity (with the attendant reduction in the concentration of $CaCO_3$ particles) as the primary cause for the shift in the zooplankton assemblage is the temporal coincidence of the changes (Fig. 1a, Womble

et al. 1996, Fig. 5). Further, the character of the shift in the assemblage is consistent with the known impacts of both salinity and $CaCO_3$ particles.

The mechanisms of impact of salinity and $CaCO_3$ particles in structuring the zooplankton assemblage are quite different. Salinity affects the osmoregulation capabilities of various species (e.g., Remane and Schlieper 1971, Wetzel 1983). While $CaCO_3$ particles can interfere with zooplankton feeding (Vanderploeg et al. 1987). Data are not available to resolve the relative roles of these soluble and particulate phase effects for Onondaga Lake. However, partitioning these effects is not important in assigning responsibility as both are largely driven by ionic waste inputs from soda ash

Table 4.–Pearson correlation coefficients for Onondaga Lake zooplankton community principal components scores and limnological parameters (numbers in parenthesis - degrees of freedom).

Parameter (df)	PC1	PC2	PC3	PC4
Total Turbidity (49)	-.62****	-.04	.30	.31
Calcite Turbidity (49)	-.29*	.11	.28	.09
Secchi depth (108)	.57****	-.21*	-.26**	-.24
DO - 10 m (108)	-.09	-.38****	.13	.12
DO - 15 m (108)	.10	-.44****	.31**	-.06
$DOz = 0$ mg-L^{-1} (108)	.12	-.49****	.22*	-.06
$DOz < 5$ mg-L^{-1} (108)	.01	-.37***	.17	.15
thermocline depth (107)	-.14	-.17	.42****	-.05
Chl *a* - 1 m (66)	-.35**	-.31*	.15	.12
Chl *a* - 4m (58)	-.26*	-.21	.15	.21
Chl *a* - 10 m (44)	-.35*	-.15	.27	.20
Mean Temp. 0 - 10 m (107)	.05	.53****	-.06	-.17

**** P < .0001
*** P < .001
** P < .01
* P < .05

production (Doerr et al. 1994, Driscoll et al. 1994, Womble et al. 1996), and abrupt reductions in both salinity (Doerr et al. 1994, Effler 1996, see Fig. 1a) and CaCO$_3$ deposition (i.e., precipitation, Womble et al. 1996) were documented following the closure of the facility. We consider the potential effects of CaCO$_3$ precipitate as part of the salinity impact, as these particles are a direct outcome of the salinity composition of this lake (Effler et al. 1986, Johnson et al. 1991, Womble et al. 1996).

High salinity is known to exert selective pressure on the zooplankton community (Remane and Schlieper 1971), with a majority of cladocera and copepoda taxa restricted to water less than 1‰ (Remane and Schlieper 1971, Fig. 1a). The probable role of the elevated salinity levels that prevailed in the lake before closure of the soda ash/chlor-alkali facility (see Fig. 1a) in limiting zooplankton diversity was first identified by Meyer and Effler (1980). Most of the common zooplankton reported for 1969 and 1978 were identified as unusually tolerant of elevated salinity (Meyer and Effler 1980). The three species that have become important to the assemblage following closure of the facility, *Daphnia galeata*, *Diaphanosoma leuchtenbergianum*, and *Diaptomus siciloides* (Fig. 3) are not considered salinity tolerant (e.g., Remane and Schlieper 1971).

The shift to increased representation by daphnids in the zooplankton assemblage of Onondaga Lake since closure of the soda ash/chlor-alkali facility is also consistent with the reduction in CaCO$_3$ particle production (e.g., Vanderploeg et al. 1987) that attended this closure (and coupled reduction in salinity; Driscoll et al. 1994, Womble et al. 1996). Mineral particles in general (Arruda et al. 1983, Hart 1988, Koenings et al. 1990), and CaCO$_3$ particles specifically (Vanderploeg et al. 1987), are known to interfere with the feeding of grazing daphnids. Mineral (or inorganic) turbidity has been shown to reduce foraging efficiency.

Cladocerans have limited ability to reject filtered (e.g., inorganic) particles, while copepods use long-range olfaction in conjunction with coordinated movements of the mouthparts to actively capture food particles (Vanderploeg et al. 1987). Vanderploeg et al. (1987) indicated that in systems with high CaCO$_3$ particle concentrations, such as Onondaga Lake (Auer et al. 1996, Johnson et al. 1991, Yin and Johnson 1984), cladocerans are at a significant competitive disadvantage. This is consistent with the observed dominance of *Cyclops vernalis* before closure of the soda ash/chlor-alkali facility (Fig. 3). Calanoid and/or cyclopoid copepods often dominate the zooplankton communities of lakes with high mineral turbidity (Koenings et al. 1990). Koenings et al. (1990) have observed that many glacial lakes have zooplankton communities consisting of a single macrozooplanktor,

a cyclopoid copepod.

Further, ingestion of CaCO$_3$ can be expected to increase respiration, owing to increased swimming effort required to compensate for the weight of mineral particles in the gut (Vanderploeg et al. 1987). The coating of cladocerans with CaCO$_3$ precipitate reported for the lake before closure of the soda ash/chlor-alkali facility (Garofalo and Effler 1987) may also have contributed to increased respiration.

We can not discount the operation of other influences in mediating the observed dramatic shifts in the zooplankton assemblage (Fig. 3). The wide range of pollution problems that impact the lake has been reviewed by Effler and Hennigan (1996). The more prominent water quality problems, such as cultural eutrophication (and certain of its manifestations) and high free ammonia concentrations, have remained relatively uniform for the period 1978-1990 (e.g., Fig. 3), and particularly over the interval (e.g., 1985-1988) of the major shift in the zooplankton assemblage (e.g., Effler et al. 1996a). A shift to reduced quantities of planktivorous fish (e.g., increase in pisivores) in the lake, coincident with the closure (and reduced lake salinity), represents an alternate explanation for the character (type and timing) of the observed shift in zooplankton (e.g., Brooks and Dodson 1965, Hutchinson 1971, Siegfried 1987). Unfortunately, detailed fish population data are not available for each year over the period of record for the zooplankton assemblage (Tango and Ringler 1996). However, published results of surveys conducted in 1980 and 1989-1990 (Tango and Ringler 1996), and unpublished data from the 1980-1989 interval (e.g., personal communication T. Chiotti, NYSDEC 1995), indicate planktivore dominance has prevailed throughout the period. Thus a change in the fish population does not seem to be a likely explanation for the observed shift in the zooplankton community. There are no indications that changes in water quality conditions, other than salinity (e.g., Effler 1996), have occurred that would explain the character (including timing) of the observed shift in the lake's zooplankton community. Based on the available information, the reduction in salinity (including the possible influence of the coupled reduction in CaCO$_3$ precipitation), that resulted from the closure of the soda ash/chlor-alkali facility, seems the most likely explanation for the shift in the zooplankton community.

Zooplankton Effects On Phytoplankton and Clarity

Analysis of concurrent monitoring data indicates the shift in the zooplankton assemblage (Fig. 3), driven
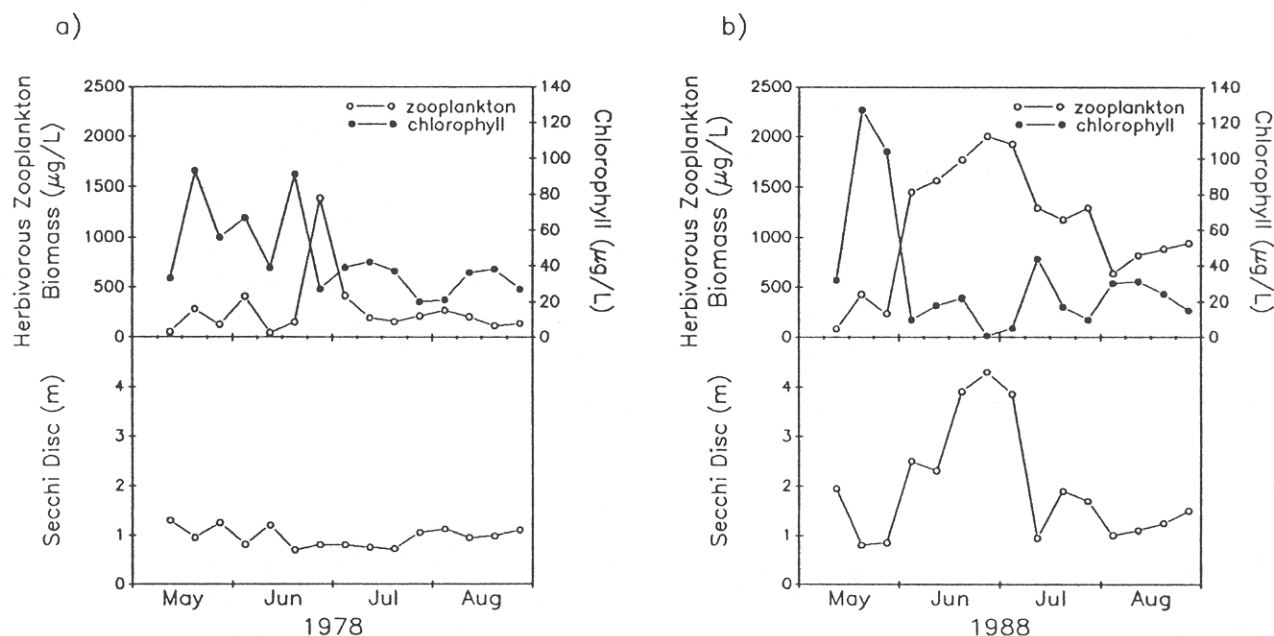
a) b)

Figure 6.–Temporal distributions of herbivorus zooplankton biomass, phytoplankton biomass and clarity (Secchi disc depth) in Onondaga Lake: a) 1978, and b) 1988.

by the closure of the soda ash/chlor-alkali facility, has caused changes in the temporal structure of phytoplankton biomass, water clarity, and phytoplankton composition. Specifically, minima in phytoplankton biomass have been lower and lasted longer (e.g., Fig. 6; Auer et al. 1996), clarity maxima have been higher and lasted longer (e.g., Fig.'s 1b and 6; Perkins and Effler 1996), and nuisance filamentous cyanobacteria (particularly *Aphanizomenon flos-aquae*) have reemerged as a dominant component of the late summer phytoplankton assemblage of the lake (Auer et al. 1996).

Increased grazing of phytoplankton in early summer in a year following closure (1988) compared to a year before closure (1978) of the soda ash/chlor-alkali facility is suggested by review of paired distributions of herbivorous zooplankton biomass (calculated as total biomass minus adult *Cyclops vernalis* biomass) and phytoplankton biomass (as chlorophyll, Fig. 6). Paired clarity data are included for the same two years (Fig. 6). In reviewing these distributions (Fig. 6), it is important to recall that the phytoplankton population of the lake remains nearly nutrient-saturated throughout the spring-fall interval (Connors et al. 1996). Thus the various decreases in phytoplankton biomass during 1978 and 1988 were not a result of nutrient-limitation effects. The sharpest decrease in chlorophyll concentration in the summer of 1978 coincides with the greatest increase in herbivorous zooplankton biomass, consistent with the effects of grazing. Note, however, that the decrease in phytoplankton biomass apparently was not great enough to result in a "clearing event" (Fig. 6a). An increased

effect of grazing on phytoplankton biomass is indicated in the 1988 (and 1987 and 1989) distributions (Fig. 6b). Small edible forms dominate the phytoplankton community of the lake before the "clearing events" (Auer et al. 1996). Note that the major (and opposite) inflections in phytoplankton and zooplankton biomass in June 1988 were accompanied by a distinct increase in transparency (Fig. 6b), and that continued increases in herbivorous zooplankton biomass in July were coincident with the further reduction in chlorophyll concentration to its seasonal minimum (much lower than observed in 1978, Fig. 6a) and the development of the maximum clarity of the "clearing event". Thus the development of the "clearing event" in 1988 (Fig. 6b; and observed annually since 1987) suggests increased grazing pressure resulting from the shift to more efficient grazers in the zooplankton assemblage (large daphnids and a calanoid, Fig. 3).

Optical measurements (Perkins and Effler 1996) and individual particle analysis (Johnson et al. 1991) indicate that the high clarities observed during the "clearing events" are not only a result of reductions in the concentrations of phytoplankton biomass, but also inorganic particles. This feature is also consistent with the shift to increased representation by daphnids in Onondaga Lake's zooplankton community, associated with the non-selective feeding of these animals.

The composition of the phytoplankton community may be strongly influenced by the selective grazing of herbivorous zooplankton (Svensson and Stenson 1991). Selection, based on algal size, shape, taste and/or abundance, removes edible phytoplankton species,

and thereby benefits inedible forms. The recent shift to a phytoplankton community dominated by *Aphanizomenon flos-aquae* in late summer (Auer et al. 1996) is consistent with the increased abundance of large daphnids. Large daphnids are extremely efficient grazers on flagellated green algae, cryptomonads, and diatoms (Svensson and Stenson 1991), and selective removal of these forms facilitates dominance by cyanobacteria. In lakes where large daphnids are an important component of the zooplankton, *A. flos-aquae* populations are generally dominated by flake-forming morphs (Andersson and Cronberg 1984, Lynch 1980, Porter 1977). These large flakes are, by virtue of their size, inedible for daphnids and interfere with food collection (e.g., Gliwicz and Siedlar 1980).

Management Perspectives

The dramatic shift that has occurred in the zooplankton assemblage of Onondaga Lake since 1987 is likely a result of a reduction in salinity brought about by closure of the adjoining soda ash/chlor-alkali facility. The shift in the zooplankton community appears to be responsible for "clearing events" observed annually in the lake since 1987, which has been perceived as a major improvement in water quality by the public. However, the reemergence of filamentous cyanobacteria and related nuisance conditions (e.g., floating "mats", decomposition along the shoreline) in response to zooplankton grazing has been viewed by the public (e.g., related coverage in the media) as a deterioration in lake conditions.

This work, and treatments of nutrient loading and in-lake conditions presented elsewhere in this issue (Connors et al. 1996, Effler et al. 1996a), indicate that the observed improvements in clarity and the reemergence of nuisance cyanobacteria in the lake are more directly linked to changes in the discharge of ionic waste (Effler et al. 1996b) than to changes in nutrient conditions. Additional changes in the zooplankton assemblage, and related features of water quality, are a distinct possibility, as the loading of ionic waste to the lake is further reduced.

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